NATURAL HISTORY MISCELLANEA

The Chicago Academy of Sciences

Lincoln Park - 2001 N. Clark St., Chicago 14, Illinois

No. 66 July 28, 1950

Aggressive Behavior in Male Sidewinders, Crotalus cerastes, with a Discussion of Aggressive Behavior and Territoriality in Snakes

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Aggressive behavior is widespread among snakes although it has not been commonly observed and little is known concerning it. The present report adds the sidewinder or horned rattlesnake, *Crotalus cerastes*, to a growing list of serpents which have been observed to exhibit aggressive behavior.

A series of six adult sidewinders, C c. laterorepens, collected at Clark Dry Lake, San Diego County, California, April 8, 1949, were placed in a three-gallon, covered, aluminum can immediately following their capture. A few hours later the snakes were heard sliding about within the container and it was opened; one individual was bleeding from a fresh fang puncture about two inches posterior to the head. A few days later these specimens were placed in a screen-fronted, hinged-top, wooden cage (20" x 12" x 11") with two other adult sidewinders collected near Indio, Riverside Co., California, April 13, 1949.

On April 25, 1949, at 9:30 A. M., thumping and sliding noises attracted attention to the box. Two of the snakes (from Clark Dry Lake) were raising the anterior portions (one-third) of their bodies vertically from the floor of the cage. They proceeded to entwine their raised bodies, suddenly to force or throw one another to the bottom of the cage, disengage, and repeat the same series of events over and over again. This behavior, a stereotyped pattern common to several serpents, continued uninterruptedly for approximately an hour and one-half. The snakes evinced no concern over the close proximity of the observers. The excellent photographs of fighting *Crotalus r. ruber* presented by Shaw (1948) suffice to show the positions assumed by the sidewinders; the pattern is nearly identical in both species as well as in other crotalids which have been observed while fighting. At the climax, the

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snakes suddenly changed tactics while parrying in the upright position and vigorously bit each other in the neck, approximately two inches posterior to the head. They then separated, waited motionlessly for approximately two minutes, and again advanced toward each other raising their necks and the anterior portions of their bodies with heads held as before, at approximately 45 degrees to the horizontal. Again, instead of the usual twining, they suddenly bit into each others' necks. * One fang of one combatant did not penetrate during the second biting and no venom was extruded from it. Moreover, no venom was seen on either snake. It appears doubtful that either ejected venom during the biting. Following the bout the participants retired to opposite ends of the cage. During the entire period of observation none of the other snakes (male and female) in the cage moved. The size of the cage was fully adequate to permit these small snakes to carry out the details of the behavior pattern.

In addition to muscular action in the anterior portions of the bodies, where the major contacts were made, similar entwining movements were occasionally noted at the posterior sections of the bodies and at the tails. The posterior parts became involved in the same general twisting and twining activity as the rest of the body and were under similar muscular tension. The posterior movements appeared to be involved in gaining leverage; they were definitely not involved in attempts at copulation as has been supposed by some observers witnessing similar behavior in other species (see Gloyd, 1948).

Both participants proved to be adult males in breeding condition. Hemipenes were everted, testes were removed and fixed. In both specimens, sections through the seminiferous tubules show spermatogenic cells in various stages of differentiation of the sexually mature testis. Snout-vent lengths and measurements of gross testis size are presented in Table I. The histological picture and the measurements of gross testis size indicate sexual maturity of the male combatants at the time of their exhibition of aggressive behavior during April. Copulation of a male and female C. cerastes was observed during the same week of April, by Raymond B. Cowles (oral communication), in the laboratory at the University of California, Los Angeles. No behavior of the aggressive type was observed.

*Ramsey (1948, p. 228) observed a pair of male Agkistrodon piscivorus leucostoma in the field, striking with mouths closed and biting each other on head and body when pinned down

Shaw (1948, p. 145) states that "The combat dance of Agkistrodon m. laticinctus is similar to that of Crotalus but differs quite markedly, insofar as our observations are concerned, in that one of the males of Agkistrodon acts as though he were afraid of being bitten on the head."

TABLE I

Crotalus atrox

*TCWC 3234 SV 957 mm. Left oviduct with 9 eggs, length 4.1 mm. to 9.9 mm. (6.7); formalin.

Right oviduct empty.

TCWC 3233 SV 1212 mm. Right testis 37.1 mm. x 11.9 mm.; formalin.

Left testis 33.6 mm. x 11.8 mm.; formalin. Ratio of mean testis length to SV length = .029.

Crotalus cerastes

*UCLA 4169 SV 614 mm. Right testis 15.5 mm. x 8 mm.; fresh.

Left testis 16 mm. x 6 mm.; fresh. Ratio of mean testis length to SV length = .026

UCLA 4170 SV 491 mm. Right testis 16 mm. x 5.5 mm.; fresh.

Left testis 13 mm. x 5 mm.; fresh. Ratio of mean testis length to SV length = .029.

Snout-vent length and gonad gross size data obtained from a male and female pair of *Crotalus atrox* observed mating on August 23, 1948 by M. H. Whisenhunt, and a male pair of *Crotalus cerastes laterorepens* observed fighting on April 25, 1949. See text.

DISCUSSION

The fighting of the adult pair of sidewinders is an additional example of intraspecific aggressive behavior in male snakes. Franke (1881) was apparently the first to record intraspecific fighting between males. Subsequent observation of such behavior has been but rarely recognized as fighting between two members of the same sex. Rather it has been considered courtship or mating behavior and commonly termed "dance." The following authors have recognized and recorded aggressive behavior in certain forms: Reuss (1923), Baumman (1929), Koster (1932), Prior (1933), McCann (1935), and Fleay (1937). In summaries of courtship and mating behavior in snakes, Davis (1937) and particularly Noble (1937) have discussed some of these reports. With regard to aggressive behavior, Davis concluded that males do not fight among themselves during the breeding season. Noble concluded that rivalry among males does occur. In recent reviews, Lowe (1948) and Shaw (1948) have attempted to bring into better focus the differences between the well differentiated aggressive behavior pattern and mating pattern of snakes.

Noble (1937) was among the first (as were McCann and Fleay) to emphasize a needed observational discrimination between the courtship patterns and intraspecific fighting patterns of snakes. He noted that the three species

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t Measurements of the gonads of C. atrox to nearest 0.1 mm.; C. cerastes to nearest 0.5 mm.

of European snakes which show sexual dichromatism (Coronella austriaca, Vipera berus, and V. aspic) also exhibit rivalry among males. He states (p. 692):

"Sexual dichromatism has developed only among those snakes in which the males fight among themselves for females. A male livery is presumably a warning to other males rather than an attraction to the female."

Noble was undoubtedly correct concerning the releaser nature of "male livery" in sexually dichromatic forms, but it is now known that the males of several species of snakes not exhibiting sexual dimorphism of color or color pattern also exhibit aggressive behavior; the fighting of male *Crotalus cerastes* as here reported is a case in point.

Noble (1937, p. 687) accepted the statement by Davis (1937) that "dancing" *Agkistrodon piscivorus* copulated, as observed in the St. Louis Zoo by R. M. Perkins, and thus stated the following:

"The courting snakes [Agkistrodon] seem to raise the anterior parts of the body much more than in Crotalus and `each snake pushes and rubs vigorously against its mate.' It is interesting that the courtship of Crotalus and Sistrurus should be so much alike and yet different from that of A. piscivorus. It would be important to know how closely the copperhead and water moccasin agree in their courtship."

These queries can be answered today. The copperhead and water moccasin exhibit the same courtship behavior as well as the same fighting pattern and, what is more revealing, these patterns are the same as those now recorded for rattlesnakes. Thus in all of these pit-vipers there is in general the same courtship-mating pattern and the same aggressive behavior pattern, and in all, the two patterns are distinct. These behavioral relationships and differences are made clear by data contained in the following reports: Guthrie (1927), Wiley (1929), Wood (1933), Noble (1937), Gloyd (1947, 1948), Lowe (1942, 1948), Ramsey (1948), and Shaw (1948). The observations by Perkins on water moccasins in the St. Louis Zoo as reported by Davis (1937), which led to Noble's queries (quoted above), were recently questioned by Shaw (1948). After a discussion of matings and "dances" of crotalids, including observations on *Agkistrodon*, Shaw (p. 138) states:

"It is suggested, then, that the observations of R. M. Perkins on A. piscivorus as reported by Davis were not continuous and that the dance was actually combat between two males. Therefore the ensuing observed copulation may have been either homosexual union, or more likely a normal mating, the female having been confused by the observer with a previously noted dancing male of similar size and markings."

A recent field observation by Whisenhunt (1949) is of interest here for it presents the first clear-cut case, as well as the only case other than that of *Agkistrodon* just discussed, in which apparently "dancing" male and female crotalids are reported to have copulated. He states:

"On August 23, 1948, about 7:00 A. M. while working on a white-tailed deer research project, I observed two diamond rattlesnakes on the Seth Martin Ranch, 12 miles south of Mason, Mason County, Texas. They were first noticed on a rocky ledge about five feet from the observer when one of the snakes began to rattle. It was noted that the snakes were already united in copulation. I slipped away as quietly as possible and went to the automobile to get a pistol. Upon returning about ten minutes later, I was extremely cautious to prevent disturbing the pair. When next observed the snakes were still united in copulation, and twined about each other with heads extending approximately 18 inches above the ground. A swaying motion of the heads was noted, but it seemed that the action was necessary in order to maintain balance while in the upright position. An almost constant peristaltic action was noted in the abdominal regions of both snakes, especially above the areas of union. During this time one of the pair was rubbing his head up and down the neck of the other, giving an impression of tender affection between the two."

Through the courtesy of M. H. Whisenhunt and Dr. W. B. Davis of the Texas Cooperative Wildlife Unit, College Station, Texas, we have examined the pair of rattlesnakes in question and have verified their sex as male and female. The performance of this pair apparently lacked the vigorous twining and throwing of bodies characteristic of the aggressive behavior of Crotalus and added a variation described as "rubbing his head up and down the neck of the other." A common property of this performance and the aggressive behavior of males is the raising of anterior portions of the body above the ground, but with only a passive twining in this case. It may be said then, that although the copulating male and female did not perform a " combat dance," they went through a part of the display of fighting males. This interesting observation is not particularly surprising, nor, of course, can it alter the established fact of a vigorous aggressive behavior between rattlesnake males, including Crotalus atrox. Its main interest lies in the fact of the partial overlap between the mating pattern and fighting pattern. Such overlap may be more common than is indicated by this single recorded observation describing it.

The reproductive states of the participants obviously has a bearing on the problem. In general, as will be mentioned again below, aggressive behavior in animals functions, among other things, to test sexual readiness of the opposite sex and is also involved in sex discrimination. Examination of the male *C. atrox* disclosed two full-sized testes (see Table I). Examination of the female disclosed nine eggs in the left oviduct ranging in length from 4.1 mm. to 9.9 mm. (6.7) in size; none present in the right oviduct.

It is also noted that the behavior recorded by Whisenhunt was observed after first disturbing the pair, although not while they lay quiet (in copulation) as when first observed. This fact may be of significance, for if the female was, or became, refractory for any reason, the normal mating procedure

may have been altered. Further speculation can serve no useful purpose. Proper interpretation of the behavior observed by Whisenhunt awaits the accumulation of additional field data of a more complete nature in which the observer's undetected observations commence prior to the meeting of the future couplet and extend at least to the complete and voluntary separation of the pair.

It can hardly be overemphasized that the distinctiveness of the mating patterns of snakes as opposed to their fighting patterns is clearly recognizable. Moreover, the uniformity of each behavioral pattern throughout major phylogenetic groups is striking. Thus as the differences between mating behavior and aggressive behavior become more apparent they clearly substantiate Noble's (1937) conclusion that "The courtship pattern of snakes has not undergone a great change in phylogeny." As will be pointed out, the aggressive behavior pattern also has undergone relatively little change.

As in crotalids, the behavior patterns of the Indian colubrid, *Ptyas mucosus*, have been confused for many years. Entwining bodies, sparring, and elevation of the anterior portions of the bodies of pairs of individuals have been observed on several occasions (Millet, 1909; Wall, 1921; Prater, 1933; and others). The observers assumed the pairs to be engaged in courtship or mating activity. McCann (1935) for the first time dissected two freshly killed *Ptyas* collected after the observation of such behavior and found both to be males. Noble (1937) was apparently unaware of McCann's report and followed the strict interpretation of such behavior of *Ptyas* as courtship or mating activity as did Davis (1937).

A similar entwining and elevation of bodies occurs in the marked aggressive behavior pattern of the Australian elapid, *Pseudechis porphriacus* (Fleay, 1937). Fleay carefully points out the characteristic differences between the fighting behavior and the more passive mating behavior of several *Pseudechis* kept under close observation. Both *Pseudechis* and *Ptyas* lack sexual dichromatism and both exhibit pronounced aggressive behavior in males.

THE FUNCTION OF FIGHTING

With regard to aggressive behavior in animals in general, Tinbergen (1936) has stressed the fact that the whole problem `has drifted away from the function of fighting to the meaning of territory." He has presented objections to the overemphasizing of "territory" as the function of fighting behavior, pointing out that fighting does not occur in the presence of territory only, and in all animals it serves to secure one or more objects or situations which are necessary for reproduction. Moreover, as Noble (1934, 1937) and others have stressed, aggressive behavior functions to test sexual readiness of 6

the opposite sex and is also often involved in sex discrimination. Stereotyped aggressive behavior patterns are important among those sign stimuli releasing social response stated by Lorenz (1935) in his original formulation of the releaser concept. Lorenz (1937, p. 249) states:

"The means evolved for the sending out of key-stimuli may lie in a bodily character, as a special color design or structure, or in an instinctive action, such as posturing, `dance' movements and the like. In most cases they are found in both, that is, in some instinctive acts which display color schemes or structures that were evolved exclusively for this end. All such devices for the issuing of releasing stimuli, I have termed releasers (Ausloser), regardless of whether the releasing factor be optical or acoustical, whether an act, a structure or a color."

Aggressive behavior and territorialism are, of course, not synonymous terms. The concepts they label are not of the same scope; the latter (like social dominance) is but a facet of the former. Aggressive behavior (but not territoriality) is now known to be widespread among snakes. On the whole it appears to be more highly developed in forms which are phylogenetically more advanced than it is in the more primitive types. The aggressive pattern of Crotalus cerastes is essentially the same as that for C. atrox (Lowe, 1942, 1948; Gloyd, 1948), Cr. ruber (Lowe, 1942; Shaw, 1948), C. viridis (Gloyd, 1947), Agkistrodon piscivorus (Carr and Carr, 1942; Ramsey, 1948; Shaw, 1948), A. mokeson (Gloyd, 1947), Vipera berus (Reuss, 1923), and V. aspis (Baumman, 1929; Koster, 1032). Similar stereotyped aggressive behavior in various but little modified form is also present in the elapids (Dendroaspis, Fitzsimons, 1919; Pseudechis, Fleay, 1937; Naja and Ophiophagus, Smith, 1939), and in aglyphous and opisthoglyphous colubrids (Coronella, Franke, 1881; Dispholydus, Fitzsimons, 1919; Ptyas, McCann, 1935; Pituophis, Woodbury, 1940). Thus as the present list includes members of the aglyphous, opisthoglyphous, proteroglyphous and solenoglyphous groups, it is clear that aggressive behavior among snakes is a trenchant, genetically controlled phenomenon the stereotyped patterns of which transgress wide ecological barriers, being evident in greatly diverse physiological and morphological types. As mentioned previously the same is true for the mating patterns of snakes. * From a study of the cases reported thus far, it is recognized that in snakes, as in lizards, aggressive behavior is an expression of competition involving, as the case may be, territoriality, and social or sexual domination; it may also be involved in sex discrimination and the testing of sexual readiness.

*Noble (1937) speaking of *Elaphe quatuorlineata* of Europe and *Elaphe quadrivittata* of North America states, "Since these two species of *Elaphe* are found on opposite sides of the Atlantic we have here a splendid case of the constancy of courtship pattern in related species regardless of the environment."

It is not yet known to what extent territoriality occurs in the majority of snakes which have been observed to exhibit aggressive behavior. Because the major portion of observations of aggressive behavior have been brief, and many were until recently erroneously considered courtship or mating behavior, there is relatively little detailed information concerning any case yet observed in nature. Thus information which might aid in determination of the precise function of fighting in snakes is still much to be desired. It seems clear that certain snakes (for example, Natrix, Thamnophis, Storeria) do not exhibit rivalry at any time, a conclusion based on the observations of numbers of individuals of different species, in and out of breeding season, in the field and in captivity (see Noble, 1937). Whereas in snakes the precise functions of fighting are not yet well understood, in the case of lizards the situation is different in that not only is aggressive behavior more frequently observed but it is also quite well understood. We can hardly agree with a recent concluding statement from D. E. Davis (1949, p. 250) 'Until more is !earned of the behavior of most reptiles, one must speak of the home range of an individual, without attempting to analyze the psychological aspects of its behavior." It seems to us that this is somewhat misleading if not undesirable as a working hypothesis. It would be obviously meaningless, for example, to speak of the aggressive behavior of male Crotalus strictly in terms of home range behavior, regardless of whether it may or may not be territorial behavior. From his analysis it would appear that this author is unaware of a considerable and growing body of data on the aggressive behavior of reptiles which thus far includes the lizards, snakes, and crocodilians.

Noble (1937) was one of the first to discuss territoriality in snakes. Not-withstanding the conclusion of Davis (1936), that male snakes do not fight among themselves during the breeding season, Noble recognized that aggressive behavior had been clearly shown for the European genera *Coronella* and *Vipera*, and stated (p. 687): `Although the male vipers, like some male lizards, usually appear earlier in the spring than do females they do not mark out definite territories which they defend against other males." During recent years there have been several studies of marked individuals of several species of North American snakes and these have been found to be sedentary, like other reptiles, occupying home ranges of varying extent (Fitch and Glading, 1947; Fitch, 1949; Imler, 1945; Stickel and Cope, 1947; Seibert and Hagen, 1947). Yet there have been no particular studies that would disclose the actual presence or absence of *territoriality* in any of these forms. Concerning the aggressive behavior of the Pacific rattlesnake (*Crotalus viridis oreganus*), Fitch (1949, p. 572) has made the following interesting observation:

"Success in vanquishing a rival in such contests may lead to success in mating. A possible instance of this was recorded early in the present study, when a large adult male rattlesnake was found dead, with post mortem evidence of snake bite, only ten feet away from a mating pair of the same species (Fitch and Glading, 1947, p. 121). It seems obvious that the occurrence of such encounters does not constitute territoriality in the same sense in which it occurs in certain birds and lizards, for instance."

Woodbury (1940) reported what appears to be a similar case of fighting involving sexual domination in *Pitnophis*. In the field at Great Salt Lake, Utah, a pair of adult male *P. catenifer deserticola* were observed in active combat in the presence of a passive adult female. The fighting involved entwining, constricting, and striking with the smaller male receiving the worst of the bout.

Aggressive behavior definitely associated with defense of area is known in certain snakes. Both the male and female king cobra (Ophiophagus) defend their nest as does Naja naja (Smith, 1939). With regard to the black mamba (Dendroaspis angusticeps) of South Africa, Fitzsimons (1919) states that as a general rule it has a secure retreat to which it retires when alarmed but that "during the pairing season these snakes are very aggressive, and will at times boldly attack anyone courageous enough to venture into their haunts." R. B. Cowles informs us (oral communication) that the Zulus of South Africa recognize the defense of a given area of "bush" by mambas and avoid it at all cost, even to the extent of rerouting their trails around these nesting sites. It is still not known to what extent mambas and cobras engage in defense of areas against individuals of their own species, although there can be little doubt that such occurs. Field study of this aspect of the natural history of cobras and their allies is, of course, much to be desired; the question to be answered is to what extent the display of cobras and mambas is aggressive behavior directed towards members of the same species, and to what extent, on the other hand, is it employed for the intimidation of other animals. The well-known hood of the cobra is extended when the snake is disturbed. The combination of its structure, mechanism, and attendant behavior is a visual releaser of unrivaled display among snakes. Spreading the hood of cobras is a part of the aggressive behavior pattern, not the mating pattern.* The aggressive black mamba also *effects* a grotesque intimidation posture. Fitzsimons (1919, p. 204) cites the observations of W. P. Jones, a resident of

"Concerning the *mating* pattern of *Naja tripudans*, Wall (1921) states: "In Mr. Hampton's vivarium coitus lasted intermittently for three days. He observed that the pair nodd ed their heads continually, and their bodies quivered They did not expand their hoods, neither did they wrap themselves around *each* other. Each turned the vent upwards and sideways to affect angagement."

Zululand in parts frequented by black mambas:

.. Black mambas have the power of apparently inflating the greater portion of the body and neck. The neck is not distended in the manner of the Cobra family, but the sides appear to be compressed together so that when seen straight on, this section of the body presents the appearance of a narrow ridge. When viewed sideways it gives the creature with its very small head a grotesque appearance. The full distension is rarely resorted to. It moves deliberately and even awkwardly, and quite unlike itself when the distension is complete, and it would be a very dangerous proceeding to molest one at such times.*

Fitzsimons (1919) shows three excellent photographs of the similar behavior of the boomslang (Dispholydus) in the act of distending the fold of loose skin of the throat and body by inflation with air. A caption under one of these photographs states: "The throat is puffed out thus when the snake is angry and defiant, and desirous of frightening its enemy." This lateral display of Dispholydus and Dendroaspis bears a remarkable resemblance to the extended chin dewlap and body compression of many lizards in which it is utilized for the same purpose. Lateral display is a common visual releaser which is found in fish, amphibians, reptiles, and birds.

SUMMARY AND CONCLUSIONS

The aggressive display of two adult male sidewinders was observed in the laboratory on April 25, 1949. The aggressive behavior of *Crotalus cerastes laterorepens* follows closely the pattern that has been described for other pit-vipers. At the climax of the fight each vigorously struck the other in the neck; fangs were employed. Histological study of sections through the seminiferous tubules of the testes of each snake, and measurements of gross testis size, indicate that the animals were in breeding condition.

Aggressive behavior of various but little modified form is common to many snakes. It has become clear that among snakes, this behavior is a trenchant, genetically controlled phenomenon the stereotyped patterns of which transgress wide ecological barriers, being evident in greatly diverse physiological and morphological types. Moreover, as the differences between the distinctly different mating behavior and aggressive behavior have become more apparent they clearly substantiate Noble's conclusion that the courtship patterns of snakes also have not undergone great change in phylogeny.

Association of aggressive behavior with defense of area is known to occur in certain snakes, most obviously in cobras and their allies. There is, however, insufficient information of the type required to determine the pre-

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^{*}Fitzsimons suggests that this behavior and appearance is probably the basis for the origin of the native-held belief in "crested mambas."

cise function, or functions, of most aggressive behavior that has been observed in snakes, including aglyphous, opisthoglyphous, solenoglyphous as well as other proteroglyphous forms. Nevertheless, it appears beyond reasonable doubt that such behavior is a manifestation of competition involving, as the case may be, (1) territoriality, (2) social domination, or (3) sexual domination. Moreover, it seems that it may also be involved in sex discrimination and the testing of sexual readiness as it is in other groups of the vertebrate series.

Certain snakes, for example Natrtx, Thamnophis, and *Storeria*, do not appear to exhibit aggressive behavior at any time. On the whole aggressive behavior appears to be more highly developed in forms which are phylogenetically more advanced than it is in the more primitive types.

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